

Figures 1-12. Dorsal and ventral views of the tarsi of the first four pairs of legs of *Lepturges angustatus* sp. n.

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**Affiliative and Sexual Differences Between a Reproductive and a
Nonreproductive Rhesus Group (*Macaca Mulatta*)**

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AFFILIATIVE AND SEXUAL DIFFERENCES
BETWEEN A REPRODUCTIVE AND A
NONREPRODUCTIVE RHESUS GROUP
(*Macaca mulatta*)

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ABSTRACT: A heterosexual group of nonreproductive rhesus (*Macaca mulatta*) containing vasectomized males was compared with a matched control group containing intact males. Comparisons were made on data collected before the birth of the first infant in the control group. Three Darwinian *a priori* hypotheses were used to predict differences between groups. The first hypothesis correctly predicted more affiliative and sexual behavior among experimental heterosexual dyads. The results did not support the second hypothesis that predicted less affiliation between experimental males. The third hypothesis correctly predicted that heterosexual affiliation and sexual behavior would occur between more of the possible heterosexual dyads in the experimental group. Two-tailed tests showed the females in the reproductive group engaged in significantly less intrasexual affiliation. The results suggest failure to reproduce has a causal influence on the affiliative and sexual interaction patterns of rhesus macaques.

Studies of differences between contracepting and noncontracepting groups of nonhuman primates may help us to understand differences between our social and sexual behavior and that of our recent ancestors. The effects of contraception on humans may be so great that studies of natural groups of nonhuman primates may not shed much light on the behavior people in developed nations (Rasmussen, 1981a; Rasmussen, 1984; Rasmussen, Reinhardt & Goy, 1987; Rasmussen, 1994).

Empirical research on the behavioral processes associated with contraception must be matched with the development of evolutionary

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theory. Most evolutionary theory describes functions of human social and sexual behavior as if contraception were not used. Males, for example, are portrayed as more sexually ardent and indiscriminate since they may invest less in offspring. Females are depicted as more reluctant to engage in sexual behavior. This is particularly true in mammals since conception results in the necessary female investment of time and energy associated with gestation and lactation (Daly & Wilson, 1983; Hinde, 1984; Grammar, 1989).

Empirical support for this evolutionary theory generally is drawn from studies where sexual behavior retains its natural link with reproduction. These studies may be on animals in their natural habitats or on people in hunter-gatherer or agrarian societies not using contraception (Wilson, 1975). If applied to a contracepting population, evolutionary theory should, but usually does not, explicitly recognize changes in the balance of costs and benefits of sexual behavior (Tooby, & Cosmides, 1990). The contracepting female who copulates, for example, has a decreased probability of incurring the costs of gestation, lactation and infant care. Other things being equal, copulation costs less to contracepting females. Females may therefore copulate with males for reasons unrelated to conception (Broude, 1993).

Evolutionary and functional theories should be developed to understand and predict the behavior of individuals in contracepting populations. Such theory permits connection of our evolutionary past with our current behavior. The theory also holds the potential of predicting how behavior may be currently adapting to the changed contraceptive environment. To initiate the development of evolutionary theory we must first understand the selective factors that led to the current "design" of behavioral interaction patterns. We then must determine how this design would react to changes in the social environment associated with contraception. Thus we need to understand the adaptive behavioral patterns of the organism in the environment in which it evolved (Rasmussen 1981b, 1988), the "environment of evolutionary adaptation or EEA" (Tooby & Cosmides, 1990). With knowledge of the adaptive design of behavior we then must build testable theories and hypotheses about how the design would alter in the face of contraception.

This experimental study of rhesus, *Macaca mulatta*, was guided by this strategy for the development of evolutionary theory. Knowledge of the function of social and sexual interactions in natural environments was combined with knowledge of the effects of hormones and nonreproductive environments on behavior to develop

testable hypotheses. A frequent criticism of evolutionary theories of behavior is that they do not generate testable hypotheses (Brigham, 1991; Wright, 1994). This is clearly wrong (Tinbergen, 1965). The hypotheses described here are generated from evolutionary theory and are both testable and tested. Conception was prevented in the experimental group by performing vasectomies on the sexually mature males.

The analyses are focused on differences between an experimental group and a matched control group. Differences between the groups were predicted with three *a priori* functional hypotheses. The hypotheses were formulated before the experiment and are derived from those previously published (Rasmussen, 1981a, 1984). The theoretical and empirical support for the hypotheses are briefly summarized. A more thorough description of the theory and review of the literature will appear elsewhere.

Hypothesis 1: More male-female affiliative and sexual behavior was predicted in the experimental group.

Theoretical bases. We predicted the members of the nonreproductive group would not behave much differently than a normal group where females had potentially reproductive sexual cycles. The contracepting social environment was therefore predicted to deceive members of the nonreproductive group to engage in sexual behavior as if it were connected with reproduction.

Intrasexual competition for access to mates, and time and energy associated with courtship and mating, selects individuals to engage in such behavior when it is likely to result in conception (Michael & Zumpe, 1988). Periovulatory periods in rhesus are accompanied by olfactory, visual, and behavioral stimuli (Keverne, 1983). More sexual and associated affiliative behavior were therefore predicted to occur in the experimental group since: First, copulation and associated affiliative behavior are precursors to reproductive success. Second, copulation is potentially risky and energetically expensive. Individuals would therefore be selected to engage in more sexual behavior when it has an apparently higher probability of leading to conception. Third, stimuli exist that are associated with ovulation. And fourth, more of these stimuli would be present in the experimental group because of the females' repeated nonpregnant menstrual cycles. In the nonreproductive group, the females' attractiveness, receptiveness and proceptivity (Beach, 1976) would all signal fertile matings were possible throughout the experiment.

Empirical bases. Females in the control group were expected to conceive. Rhesus sexual behavior decreases after conception (Chambers & Phoenix, 1982; Wilson, Gordon, & Chikazawa, 1982; Hill 1986). The males in the experimental group could not fertilize the females. The females would therefore have repeated nonpregnant ovulatory cycles and a breeding season of greater length (Mallow, 1981). Experimental females would therefore have more periovulatory days than their controls. Rhesus sexual behavior and heterosexual grooming are usually found to occur at highest rates during periovulatory days (Gordon, 1981; Michael & Zumpe, 1988, Hill, 1986).

Hypothesis 2: Less affiliation between males was predicted the experimental group.

Theoretical bases. More heterosexual affiliative and sexual interactions in the experimental group were predicted by hypothesis 1. These interactions were expected to be accompanied by more competition between males and therefore with less affiliation.

Hypothesis 2 is based on a theoretical continuum. This continuum is of the degree to which interactions may be competitive, and decrease the recipient's inclusive fitness, or beneficial, and increase the recipient's inclusive fitness (Rasmussen, 1988). The term beneficial is used to encompass altruism, cooperation, helping (Brown, 1983) and other behavioral patterns that increase the recipient's inclusive fitness. Patterns of affiliation are used as measures of beneficial behavior.

Empirical bases. A previous study that compared a heterosexual group of bonnet macaques (*M. radiata*) in which all females were ovariectomized and a matched control group containing intact females found that there was more agonistic behavior and less affiliation between males housed with the intact and sexually cycling females (Rasmussen, 1984). Aggression between rhesus males has also been shown to increase during breeding seasons (Wilson & Boelkins, 1970; Gordon, Rose, & Bernstein, 1976).

Females are excluded from hypothesis 2 for a theoretical reason: Aggression between females might not be expected to be greatest during sexual behavior. There are other periods in the female reproductive cycle when aggression received by females could have a stronger negative impact on their reproductive success (Silk, Clark-Wheatley, Rodman, & Samuels, 1981; Small & Smith, 1982; Michael & Zumpe, 1984). More information is needed on changes in

affiliation between females as a function of their reproductive cycle. Female-female affiliation is therefore compared between groups and subjected to two-tailed tests of significance.

Hypothesis 3: Affiliative and sexual liaisons were predicted to form between a greater proportion of the possible heterosexual dyads in the experimental group.

Theoretical bases. When copulation does not result in conception, both males and females might increase their reproductive success by copulation with different partners since their previous mates, rather than themselves, could be sterile (Rasmussen, 1981a). In the face of failure to reproduce, an adaptive response of an organism thus would be to increase the number of heterosexual partners in sexual liaisons since copulation with previous partners did not result in conception.

This hypothesis was formulated since the experimental group was expected not to be entirely deceived into acting as if sexual behavior results in conception. Feedback information does show intersexual affiliation and sexual behavior do not have a reproductive payoff: In an intact group most ovulating females conceive during their first few sexual cycles. Repeated nonpregnant ovulatory cycles are not the norm in the EEA (Short, 1974). Instead most of a rhesus female's life is spent either pregnant or lactating. Macaques may prefer some sexual partners over others (Zumpe & Michael, 1989; Huffman, 1991). If hypothesis 3 were not true, then it is possible that increased sexuality in the experimental group predicted by hypothesis 1 would result in more sexual activity between the same preferred sexual partners. Hypothesis 3 predicts, instead, that the increased sexuality associated with failure to reproduce will be associated with a greater variety of sexual partners.

Empirical bases. The presence of sterile or sub-fecund individuals could exert selective pressure for a tendency to form liaisons with more individuals. Menarche may precede initiation of ovulation in rhesus (Schwartz, Wilson, Walker & Collins, 1988). Mounts and intromissions may therefore occur during pubertal sterility. Pubertal sterility thus could select for this hypothesized tendency. The occurrence of sterile and sub-fecund adult macaques is documented (Small, 1982; Lindburg, 1983, Walker, 1995). Evidence suggests they have existed in natural troops during evolution (Moore & Ali, 1985). Sterile and sub-fecund adults also could select for this hypothesized tendency. Repeated miscarriages and infant deaths due

to the many possible mortality factors (Dittus, 1980) and other sources of variation in female reproductive success (Hrdy, 1986) would also select for liaisons with different partners (Rasmussen, 1981a).

Hypothesis 3 is consistent with decreased sexual behavior observed between rhesus pairs. These pairs were placed together weekly over a 3½ year period (Michael & Zumpe, 1978) and the females did not conceive.

Strong correlations between fertility and both marital stability and duration have been consistently reported in human demographic literature (Rasmussen, 1981a). We are only distantly related to rhesus and often form sexual, reproductive and infant care pair-bonds of much longer duration than rhesus consortships. The persistent finding of these relationships in many populations with the large sample sizes provided by censuses indicates, however, that in at least one species of primate, *Homo sapiens*, there is a correlation between the duration and stability of an affiliative and sexual relationship, marriage, and reproduction. There are, of course, difficulties in determining the causality of these correlations (Bumpass & Sweet, 1972). These difficulties underscore the need of experimental and comparative studies of nonhuman primates. Such studies may help determine the causality of behavioral processes associated with differences in number of offspring born per female.

METHOD

Group Composition and Subject Matching

The experimental group was composed of a 5-year-old vasectomized male, a 4-year-old vasectomized male, an intact 2-year-old male, four 4-year-old females, one 3-year-old female and three 2-year-old females. The control group was sex and age matched. Young rhesus were used so experimental subjects could be more closely matched to their paired controls by previous social experience. All females were nulliparous and therefore did not vary in parturitional, lactational, or infant rearing experience.

The 5 and 4-year-old males in both groups engaged in adult ejaculatory mounts of females and the 3-year-old female in the control group conceived. While young, all group members, except 2-year-olds, were sexually mature to the extent that they could potentially reproduce.

The females were selected from those who could be most closely

matched by age, weight and housing history. One of each pair of matched female subjects was randomly assigned to the experimental or control group.

Vasectomies were used to prevent reproduction since they have less direct effects on the hormones and behavior of the sterilized male (Phoenix, 1973) than other methods. Vasectomy of the two potentially reproductive males was also the procedure that could be used on the fewest subjects and yet prevent conceptions in the nonreproductive group. Group differences could therefore be most directly attributed to the differences in the reproductive cycles of the females: In the control group the females would experience repeated nonpregnant ovulatory cycles. In the experimental group the matched controls of the females were expected to rapidly conceive.

The vasectomized males were matched to controls by age, housing history, size and estimated agonistic rank in previous social groups. The vasectomies were done on the experimental 5 and 4-year-old males 3 months before data collection.

Hypothesis 1 was based on our expectation that the experimental females would have more nonpregnant ovarian cycles. This expectation was fulfilled: All 3 and 4-year-old females in the experimental group menstruated and there were 24 ovarian cycles in that group. The females experienced a mean of 4.8 ovarian cycles ($SD = 2.17$). In the control group all but one sexually mature female rapidly conceived. Three of the five conceived during their first ovarian cycle. There were only 4 ovarian cycles in the control group. Both of the two control females observed to menstruate were 4-year-olds. One had three ovarian cycles and the other had one cycle before conception. Sexually mature control females experienced a mean of 0.8 ovarian cycles ($SD = 1.3$).

Housing

The identical indoor chain-link pens housing the groups were 6.7 m long, 2.5 m wide and 2.6 m in height. Lights were turned on at 6 am and turned off at 6 pm. Two frosted windows next to the pens let in ambient light.

More sexual behavior was expected to occur in the experimental group containing females with continuous nonreproductive ovulatory cycles. This could potentially influence the males' testosterone level (Vandenbergh & Drickamer, 1974). The control group was housed close to groups containing cycling females to control this potential group difference. Housing all male rhesus groups near heterosexual

groups results in a seasonal increase of levels of testosterone in the all male groups. This increase is indistinguishable from levels in heterosexual groups (Gordon, Bernstein & Rose, 1978). The groups were housed in adjacent pens separated by a minimum distance of 1.2 m. The pens were in a room housing two additional identical pens containing breeding rhesus groups.

Rhesus sexual behavior during the breeding season is associated with increased male testosterone (Gordon, Rose & Bernstein, 1976). The groups were therefore simultaneously observed from the peak of the breeding season (January 2) to the onset of the birth season (June 1).

Behavioral Variables

Rationale

The hypotheses are based on influences of behavior on reproductive success and inclusive fitness. Ideal behavioral measures used to test these hypotheses would have only positive or negative influences on fitness. The actual influence of a behavior on fitness is, however, influenced by social and environmental context. A behavior may be sexual in one context, affiliative in another and aggressive in a third. Theoretically defined concepts such as sexual and beneficial behavior may therefore only be imperfectly assessed with empirical measures.

The measures selected were those that seemed to most accurately assess affiliative, sexual, and beneficial behavior as used in the a priori hypotheses. An evaluation of the relationships between the affiliative variables, and the influence of social context on their interrelationships has been published elsewhere (Rasmussen, 1994).

A functional definition of sexual behavior was used (Scott, 1956; Tinbergen, 1965): Sexual behavior is behavior that has been associated with conception in the EEA, the environment of evolutionary adaptation (Rasmussen, 1984). Although it may be impossible to find a behavioral pattern that has only beneficial consequences, typical measures of affiliation do assess interactions that may benefit the recipient (Crooks & Rasmussen, 1991). Affiliative behavioral patterns were therefore used to assess beneficial behavior.

Sampling

All behavioral data was collected by the author. Observations used in the analyses were collected until the day before the birth of

the first infant in the control group. Sampling sessions were conducted for 14 min on individual focal subjects. During sampling sessions, focal samples (Altmann, 1974) were collected on variables requiring constant monitoring of the subject. Concurrent sampling (Hausfater, 1975) was conducted of all occurrences (Martin & Bateson, 1993) of behavioral variables that could be accurately assessed for all group members. Instantaneous, frequency and 1/0 sampling methods (Altmann, 1974) based on 2 min intervals were used to assess the variables. The data base used here has 163 hours of 2 min interval samples collected during 14 min sampling sessions. Further description of the sampling methods appear elsewhere (Rasmussen, 1993, 1994).

Matching of Subjects and Dyads

Tests of the hypotheses require comparison of experimental and control subjects. Each subject in the experimental group was matched to a subject in the control group. Comparisons could therefore be made between subjects matched by sex and age.

Most of the comparisons between groups used here are comparisons of the interactions between pairs of individuals matched between groups. For example, the oldest male in the experimental group was matched with the oldest male in the control group. The oldest experimental female was also matched with the oldest control female. Comparisons could therefore be made between the matched dyads composed of the oldest experimental male and female and the oldest control male and female. Hypothesis 1, for example, predicts more male-female affiliative and sexual behavior in the experimental group. Application of this hypothesis led to the prediction that heterosexual dyads in the experimental group should engage in more affiliative and sexual behavior than the dyads to whom they were matched in the control group. The oldest female in the experimental group was therefore expected to groom the oldest male in that group more than the oldest female in the control group groomed the oldest male in that group.

Directional dyadic interactions are matched between groups by the age and sex of subjects within dyads. The directional dyad composed of 5-year-old male => 4-year-old male interactions in the experimental group was, for example, matched to the identical directional dyad in the control group¹. It was therefore possible to determine if, as predicted by hypothesis 2, the 5-year-old experimental male groomed the 4-year-old experimental male less than the 5-year-old control male groomed the 4-year-old control male. There were 110 possible

matched directional dyads (11 subjects x 10 cage mates in each group). Directional dyadic interactions were compared between groups for the variables ALF, grooming, grooming presents, presents, mounts, and ejaculation.

Distances between individuals are not directional since the mean distance of "A"=>"B" is the same as the mean distance of "B"=>"A". There were 55 matched non-directional dyads "A"=<=>"B" that could be compared in the two groups for the distance variables. The direction of consorts were not scored since they were due to the behavior of both the male and female.

Neither the recipients of threatening away nor the consort partners from whom the threats were directed away were recorded. Comparisons of threatening away were therefore made between matched subjects.

Variable Descriptions

Many of the variables, or variables like them, are among those most frequently found in studies of sexual and affiliative behavior of nonhuman primates. The time and space is taken here to describe these variables since nuances of variable definition, their sample and the descriptive statistics used to summarize the variables can have a substantive influence on results and their interpretation. The variables, the unit of observation and the sampling used to assess the variables are listed in Table 1. Further description of the variables, and references to previous use of the variables, appear elsewhere (Rasmussen 1984, 1993, 1994).

Neighbor distances. Distances between individuals have been used as indirect measures of affiliation since Galton (1884). Mean distance between macaques has been shown to correlate strongly and negatively with affiliative interactions (Rasmussen, 1984): individuals whose mean nearest neighbor distance is small tend to engage in more affiliative behavior.

Instantaneous samples of the coded estimated distance of the nearest neighbor male and female to the focal subject were collected at the beginning of each 2 min interval. The coded distances were as follows: 0=contact, 1=not touching to 1/3m, 2=1/3-2/3m, 3=2/3-1m, 4=1-4/3m, 5=4/3-5/3m, 6=5/3-2m, 7=greater than 2m. When

1. => indicates a directional behavioral interaction. Male grooms of females are indicated as male => female grooming. <=> is used to indicate bidirectional behavior or a measure of the distance between a dyad. When, for example, analyses are focused on grooming of males by females and grooming of females by males this is indicated as male <=> female grooming.

Table 1. Variables, Observation Unit and Sampling Method. Focal: the focal subject of the 14 minute sampling session; group: all individuals in the focal subject's group.

| Variable | Observation Unit | Sampling Method |
|---|------------------|--------------------------|
| Nearest Neighbor Distance (NN) | focal | instantaneous |
| Close Distance to Nearest Neighbor (CD) | focal | instantaneous |
| Approaches, Leaves & Follows (ALF) | focal | frequency |
| Grooming | group | concurrent 1/0 |
| Grooming presents | focal | frequency |
| Presents | focal | frequency |
| Mounts | group | concurrent frequency |
| Consorts | group | 1/0 per sampling session |
| Threatening away | group | concurrent frequency |
| Ejaculation | group | concurrent frequency |

individuals were engaged in agonistic behavior with the focal subject they were excluded as nearest neighbors since neighbor distances were used to assess affiliation (Rasmussen, 1984).

Two measures of mean distance were calculated: Nearest neighbor distance (NN) was the mean ordinal distance between a given dyad across all samples. When the focal subject had a nearest neighbor all other group members of the same gender as the nearest neighbor were given a coded distance of 7 from the focal subject for that 2 min interval. Close neighbor distance (CD) was the mean distance between a dyad during those intervals when members of the dyad were nearest neighbors. NN was thus a measure of the distance between a dyad during all sampling and CD a measure of the mean distance between individuals when they were nearest neighbours.

Approaches, leaves and follows (ALF). Approaches, leaves and follows are sensitive measures of rhesus affiliation (Chapais, 1986). The frequency of these variables was assessed for focal subjects during the 2 min intervals. These three strongly and positively correlated variables (Rasmussen, 1994) were combined in a composite variable, ALF. ALF rates were calculated as the number of times "A" approached , left or followed "B" divided by the focal samples on "A" and "B".

Grooming. Grooming, picking through the hair or skin of another with fingers or teeth (Rasmussen, 1984), was also used to assess affiliation. Data on grooming were collected with 1/0 concurrent sampling. Rates of 1/0 "A" => "B" grooming were calculated by dividing the sum of intervals with "A" => "B" grooming by the number of 2 min intervals of observation on their group.

The focus of the analyses is neither on true frequencies nor durations. The focus is on differences between matched directional dyads. Since 1/0 samples are strongly correlated with both true frequencies and durations (Martin and Bateson, 1986), differences between groups assessed with 1/0 samples, true frequencies, and durations seem likely to be in same direction.

Grooming presents. An "A"=>"B" grooming present was recorded when "A" approached "B" and exposed a body part at 1/3 m or less of "B's" hands or mouth. The frequency of grooming presents involving the focal subject was assessed throughout the 2 min intervals. Grooming present rates were calculated as the number of times "A" grooming presented to "B" divided by the focal samples on "A" and "B".

Presents. An "A"=>"B" present was scored when "A" oriented its anogenital region towards the face of "B" when "B" was within 2 m of "A". Present rates were calculated as the number of times "A" presented to "B" divided by the focal samples on "A" and "B".

Mounts. An "A"=>"B" mount was scored when "A" climbed on top of "B", placed both hands on "B"'s back and the anogenital regions of "A" and "B" were aligned as during copulation. Concurrent samples were collected on the frequency of all mounts in the focal subject's group. Rates of "A" mounting "B" were calculated as sum of these mounts divided by the 2 min intervals during which their group was observed.

Intrasexual presents and mounts were used as measures of affiliation. Heterosexual presents and mounts (Michael, Wilson & Zumpe, 1974) were used as measures of affiliative and sexual behavior. These behavioral patterns were correlated with the other measures of affiliation used here (Rasmussen, 1994).

Consorts. A consort was recorded when a male was the nearest neighbor of a female for at least 5 min and the female's sexual skin indicated she was near the middle of her menstrual cycle (Czaja et al. 1977). The dyads in consort were recorded once each 14 min sampling session. Rates of "A" <=> "B" consorts were calculated by dividing their sum by the 14 min sampling sessions conducted on their group.

Threatening Away. Threatening away is strongly associated with the initiation of sexual interactions in rhesus (Zumpe & Michael, 1970). Threatening away was scored for "A" when "A" and "B" were in consort, separated by less than 1 m and a threat away from "B" was made by "A". The threat could be an eye threat or a yawn threat. When "A" eye threatened it raised its eyebrows, flattened its ears against the side of its head and stared. When "A" yawn threatened, it yawned with its mouth open and lips retracted so as to expose its teeth. The threat could also be a hand slap, head bob, or head duck as defined by Zumpe & Michael (1970). Recipients of threats were not recorded, as threatening away was sometimes not directed at another individual. Concurrent samples were collected on the frequency of threatening away by each individual in the focal subject's group. "A's" threaten away rate was the number of times "A" threatened away divided by the sum of the 2 min intervals during which "A's" group was observed.

Ejaculation. Ejaculation was recorded if a male paused after several penis thrusts into a female's vagina and maintained a rigid posture for 5 s or more or if, after intromission, fresh ejaculate was observed on the male's penis or the female's vagina. Concurrent samples were collected on the frequency of all ejaculations in the focal subject's group. The rate of "A"'s ejaculation in "B" was calculated as the sum of these ejaculations divided by the 2 min intervals during which their group was observed.

Tests of the Hypotheses

The ability of the three combined hypotheses to predict differences between groups was evaluated with a one-tailed sign test (Siegel & Castellan, 1988). The datum tested was whether a difference between groups was in the direction predicted by an a priori hypothesis. For example, hypothesis 1 predicted the oldest female in the experimental group would groom the oldest male in that group more than the oldest female in the control group groomed the oldest male in that group. The sign of this difference in rate of grooming between groups was positive. This comparison of matched dyads therefore supported hypothesis 1.

The data used to test the hypotheses were independent: Making a correct or incorrect a priori prediction of a difference between groups did not influence the likelihood of another prediction being either correct or incorrect.

An initial overall sign test was applied to the number of correct

predictions of differences between the experimental and control groups in (a) directional variables between the 110 matched directional dyads, (b) distance variables between the 55 matched non-directional dyads, (c) differences in threaten away between the 11 matched pairs of subjects and (d) the number partners in liaisons formed for each variable used to assess hypothesis 3. The significance of the initial overall test is used to protect the experimentwise significance level. In a manner analogous to the Fisher's protected t-test, subsequent tests of hypotheses 1 and 2 are only made if the overall test of the accuracy of the hypotheses is significant (Rasmussen, 1984).

Hypothesis 3 is focused on differences in the number of pairs that formed heterosexual affiliative and sexual liaisons in the experimental and control groups. The number of pairs who were ever close neighbors was the distance variable used to assess hypothesis 3, since all individuals had NN distances. The Wilcoxon matched-pairs signed-ranks test (Siegel & Castellan, 1988) was used to assess hypothesis 3.

The hypotheses were derived from theory concerned with intrasexual competition and the reproductive function of heterosexual affiliation and sexuality. The hypotheses therefore might be more accurate when restricted to sexually mature individuals. The hypotheses were therefore applied to these individuals after the accuracy of the hypotheses was assessed for all group members.

Affiliation Between Females

The significance of differences between groups in affiliation between females was determined with two-tailed sign tests. The data tested therefore shift from correct or incorrect predictions of group differences to the direction of differences between groups. Differences between groups are not necessarily independent: Interactions between one pair of individuals are socially and physiologically associated with interactions these individuals have with group members (Michael & Zumpe, 1988) or with other groups (Gordon, Bernstein & Rose, 1978).

The sign test does not assume outcomes are independent. It is used to determine if observed outcomes differ significantly from those of the binomial distribution (Sokal & Rohlf, 1981). There are many textbook examples of applications of the sign test to outcomes unlikely to be independent. These include repeated qualitative judgments by a group (Siegel & Castellan, 1988), successive choices

by a person in an experiment (Edwards, 1972), and presence of contagious disease in groups of insects (Sokal & Rohlf, 1981).

Statistical Control of Previous Familiarity

The groups were not perfectly matched by previous familiarity (Rasmussen, 1993). Regression was used to statistically control this nuisance variable. All variables were regressed on the linear and quadratic aspects of previous familiarity as measured by the mean of number of days dyads had been housed together before the experiment. Only grooming was strongly associated with the quadratic aspect of previous familiarity (linear $r=+0.27$; linear and quadratic multiple $R= +0.34$). Residuals from the regression of grooming on both linear and quadratic aspects of previous familiarity were therefore used in the analyses. For all other variables the residuals from regression on the linear aspect of previous familiarity were used in the analyses. The relationships between the variables and previous familiarity are tested for significance and interpreted elsewhere (Rasmussen, 1993).

RESULTS

Of the 295 applications of the hypotheses to differences between groups, 183 (62%) were correct ($p<.001$). When applied to sexually mature group members, 101 of 153 applications of the hypotheses (65%) were correct ($p<.001$).

Hypothesis 1

Experimental heterosexual dyads had higher rates of affiliative and sexual behavior in 63% of the between group comparisons (Table 2). Heterosexual grooming, grooming presents, and presenting occurred at significantly higher rates in the experimental group. For all variables except CN distance more of the heterosexual dyads in the experimental group had higher levels of affiliative and sexual behavior.

There were higher rates of affiliative and sexual behavior in 69% of the experimental heterosexual dyads composed of sexually mature individuals ($p<.0001$, Table 3). ALF and presents occurred at higher rates in significantly more of the experimental dyads. For all the variables more of the experimental dyads had higher rates of

Table 2. Tests of Hypothesis 1: More Heterosexual Affiliative and Sexual Behaviour in the Experimental Group. Data are shown for all Heterosexual Dyads. Correct/Incorrect: the number of differences between groups that were in the direction predicted compared to the number of differences between groups that were not in the direction predicted; Proportion Correct: the number of correct predictions divided by the number of predictions; p Value: the probability of obtaining this number of correct predictions by chance alone; *: $p < .05$.

| Corrected Variable (Residualized on Days Together) | Correct/ Incorrect | Proportion Correct | p value |
|---|-----------------------|-----------------------|-------------|
| 1. Nearest Neighbor Distance | 14/10 | .58 | 0.2707 |
| 2. Close Neighbor Distance | 10/13 | .44 | not tested |
| 3. ALF Rate | 25/18 | .58 | 0.1801 |
| 4. 1/0 Grooming Rate | 30/16 | .65 | 0.0277* |
| 5. Grooming Present Rate | 21/10 | .68 | 0.0365* |
| 6. Present Rate | 25/11 | .69 | 0.0152* |
| 7. Mounting Rate | 19/13 | .59 | 0.1884 |
| 8. 1/0 Consort Rate | 5/2 | .71 | 0.2266 |
| 9. Threatens Away Rate | 4/0 | 1.00 | 0.0625 |
| 10. Ejaculation Rate | 5/2 | .71 | 0.2266 |
| Overall Sign Test | 158/95 | .63 | $p < .0001$ |

affiliative and sexual behavior than their matched controls.

The greatest proportion of correctly predicted differences were for the variables most closely associated with conception: consorts (71%), threaten away (100%) and ejaculation (71%). These sexual behavior patterns only occurred between adults. These variables were not significantly different between groups since they occurred between only a few individuals. When these variables are pooled they occurred at higher rates in significantly more of the matched dyads in the experimental group (14 of 18 matched dyads, $p=0.015$).

Adult female => adult male affiliative and sexual behavior occurred at higher rates in the experimental group in only 60% of the interactions ($p>.05$). Adult male => adult female affiliative and sexual behavior occurred at higher rates in 74% of the experimental dyads (Table 4, $p<.001$). When ejaculations are excluded so these interactions include the same variables as those directed by

Table 3. Tests of Hypothesis 1: More Heterosexual Affiliative and Sexual Behaviour in the Experimental Group. Data from all sexually mature dyads. See Table 2 for explanation of column labels. Consorts, Threatens Away and Ejaculations are identical to Table 2 since they only occurred in dyads not containing 2 year olds.

| Corrected Variable (Residualized on Days Together) | Correct/ Incorrect | Proportion Correct | p Value |
|---|-----------------------|-----------------------|---------|
| 1. Nearest Neighbor Distance | 8/2 | .80 | 0.0547 |
| 2. Close Neighbor Distance | 6/4 | .60 | 0.3770 |
| 3. ALF Rate | 4/5 | .74 | 0.0318* |
| 4. 1/0 Grooming Rate | 14/6 | .70 | 0.0577 |
| 5. Grooming Present Rate | 11/7 | .61 | 0.2403 |
| 6. Present Rate | 14/5 | .74 | 0.0318* |
| 7. Mounting Rate | 10/8 | .56 | 0.4073 |
| 8. 1/0 Consort Rate | 5/2 | .71 | 0.2266 |
| 9. Threatens Away Rate | 4/0 | 1.00 | 0.0625 |
| 10. Ejaculation Rate | 5/2 | .71 | 0.2266 |
| Overall Sign Test | 91/41 | .69 | p<.0001 |

Table 4. Tests of Hypothesis 1: More Heterosexual Affiliative and Sexual Behaviour in the Experimental Group. Behaviour Directed by Adult Males to Adult Females. See Table 2 for explanation of column labels.

| Corrected Variable (Residualized on Days Together) | Correct/ Incorrect | Proportion Correct | p Value |
|---|-----------------------|-----------------------|---------|
| 3. ALF Rate | 7/2 | .78 | 0.0899 |
| 4. 1/0 Grooming Rate | 7/3 | .70 | 0.1719 |
| 5. Grooming Present Rate | 7/2 | .78 | 0.0898 |
| 6. Present Rate | 8/2 | .80 | 0.0547 |
| 7. Mounting Rate | 6/3 | .67 | 0.2539 |
| 10. Ejaculation Rate | 5/2 | .71 | 0.2266 |
| Overall Sign Test | 40/14 | .74 | p<0.001 |

Table 5. Tests of Hypothesis 2: Less Affiliative Behaviour Between Males in the Experimental Group. Data from all Dyads. See Table 2 for explanation of column labels.

| Corrected Variable (Residualized on Days Together) | Correct/ Incorrect | Proportion Correct |
|---|-----------------------|-----------------------|
| 1. Nearest Neighbor Distance | 2/1 | .67 |
| 2. Close Neighbor Distance | 3/0 | 1.00 |
| 3. ALF Rate | 4/2 | .67 |
| 4. 1/0 Grooming Rate | 4/2 | .67 |
| 5. Grooming Present Rate | 3/2 | .60 |
| 6. Present Rate | 1/4 | .20 |
| 7. Mounting Rate | 1/4 | .20 |
| Overall Sign Test | 18/15 | .55 ($p=0.3639$) |

adult females to adult males, 75% of the comparisons were greater in the experimental group.

Only 43% of the experimental dyads composed of an immature male and a mature female had higher rates of affiliative and sexual behavior than their matched controls ($p>.05$). In adult male and immature female dyads, 61% of the experimentals engaged in higher rates of affiliative and sexual behavior ($p>.05$). There were higher rates of affiliative and sexual behavior in the experimental group in 65% of the dyads composed of immature males and immature females ($p>.05$).

Hypothesis 2

There was less affiliation between experimental males in 55% of the dyadic comparisons (18 of 33, $p>.05$, Table 5). Further tests were not conducted since the initial test was not significant.

Descriptive analyses of the data were conducted: Counter to hypothesis 2, there was more affiliation between the sexually mature experimental males for every variable except close neighbor distance. As predicted by hypothesis 2, in the experimental group there was less affiliation between the immature male and the two older males for all variables except presents and mounts.

Table 6. Tests of Hypothesis 3: More Heterosexual Liasons in Affiliative and Sexual Behaviour in the Experimental Group. Difference: is the difference between the residualized number of pairs who interacted by each variable in the experimental and control groups. A positive difference is in the direction predicted, that is, more liaisons formed in the experimental group. The number of pairs was residualized on the mean number of days the dyads had spent together before the experiment. **: $p < .01$.

| All Dyads | EXPERIMENTALS | CONTROLS |
|--|---------------------------|--|
| Corrected Variable | Difference from all Pairs | Difference between Sexually Mature Pairs |
| 2. Close NN | 0.67 | 1.34 |
| 3. ALF | 4.07 | 4.39 |
| 4. 1/0 Grooming | 1.21 | 8.50 |
| 5. Grooming Presents | -0.02 | 3.23 |
| 6. Presents | 2.31 | 7.61 |
| 7. Mounting | 3.23 | 6.62 |
| 8. 1/0 Consorts | 3.88 | 7.45 |
| 9. Threat Away | 2.57 | 3.22 |
| 10. Ejaculations | 3.88 | 7.45 |
| Wilcoxon matched pairs signed-ranks test | $p=0.0055^{**}$ | $p=0.0039^{**}$ |

Hypothesis 3

More heterosexual dyads in the experimental group formed affiliative and sexual liaisons for eight of nine variables ($p=0.0055$, Table 6). There were more liaisons between experimental adult dyads for all nine variables ($p=0.0039$).

Affiliation Between Females

There was significantly more affiliation between experimental females in 56% of the matched dyads (Table 7). Presents and mounts occurred at significantly higher rates in more of the experimental dyads.

Table 7. Differences between Matched Female-Female Dyads in the Experimental Group and those in the Control Group for all Dyads.*: $p < .05$; **: $p < .001$.

| Corrected Variable (Residualized on Days Together) | Correct/ Incorrect | Proportion Correct | <i>p</i> Value |
|---|-----------------------|-----------------------|----------------|
| 1. Nearest Neighbor Distance | 11/17 | .39 | 0.3447 |
| 2. Close Neighbor Distance | 10/18 | .36 | 0.1859 |
| 3. ALF Rate | 30/25 | .55 | 0.5896 |
| 4. I/O Grooming Rate | 32/21 | .60 | 0.1696 |
| 5. Grooming Present Rate | 16/23 | .41 | 0.3367 |
| 6. Present Rate | 38/12 | .76 | 0.0004*** |
| 7. Mounting Rate | 29/13 | .69 | 0.0206* |
| Overall Sign Test | 166/129 | .56 | 0.0361* |

Table 8. Differences between Matched Female-Female Dyads in the Experimental Group and those in the Control Group. Data for 3 and 4 year old female <=> 2 year old female. See Table 2 for explanation of column labels. *: $p < .05$; **: $p < .01$.

| Corrected Variable (Residualized on Days Together) | Correct/ Incorrect | Proportion Correct | <i>p</i> Value |
|---|-----------------------|-----------------------|----------------|
| 1. Nearest Neighbor Distance | 4/11 | .27 | 0.1185 |
| 2. Close Neighbor Distance | 5/10 | .33 | 0.3018 |
| 3. ALF Rate | 15/14 | .52 | 1.0000 |
| 4. I/O Grooming Rate | 17/10 | .63 | 0.2482 |
| 5. Grooming Present Rate | 9/7 | .56 | 0.8036 |
| 6. Present Rate | 20/4 | .83 | 0.0015** |
| 7. Mounting Rate | 15/2 | .88 | 0.0023** |
| Overall Sign Test | 85/58 | .59 | 0.0297* |

Affiliation between experimental adult females occurred at higher levels in 51% of the comparisons ($p > .05$). Affiliation between immature females occurred at higher levels in the experimental group in 63% of the comparisons ($p > .05$). Affiliative behavior was greater between experimental adult and immature females in more of the matched dyads (59%, $p < .05$, Table 8). Presenting and mounting

Table 9. Differences between Matched Female-Female Dyads in the Experimental Group and those in the Control Group. Data for 3 and 4 year old females => 2 year old females. See Table 2 for explanation of column labels.

| Corrected Variable (Residualized on Days Together) | Correct/ Incorrect | Proportion Correct | p Value |
|---|-----------------------|-----------------------|---------|
| 3. ALF Rate | 9/6 | .60 | 0.6072 |
| 4. 1/0 Grooming Rate | 8/6 | .57 | 0.7905 |
| 5. Grooming Present Rate | 5/4 | .56 | 1.0000 |
| 6. Present Rate | 10/2 | .83 | 0.0386* |
| 7. Mounting Rate | 7/0 | 1.00 | 0.0156* |
| Overall Sign Test | 39/18 | .68 | 0.0231* |

Table 10. Differences between Matched Female-Female Dyads in the Experimental Group and those in the Control Group. Data for 2 year old females => 3 and 4 year old females. See Table 2 for explanation of column labels.

| Corrected Variable (Residualized on Days Together) | Correct/ Incorrect | Proportion Correct | p Value |
|---|-----------------------|-----------------------|---------|
| 3. ALF Rate | 6/8 | .43 | 0.7905 |
| 4. 1/0 Grooming Rate | 9/4 | .69 | 0.2668 |
| 5. Grooming Present Rate | 4/3 | .57 | 1.0000 |
| 6. Present Rate | 10/2 | .83 | 0.0386* |
| 7. Mounting Rate | 8/2 | .80 | 0.1094 |
| Overall Sign Test | 37/19 | .66 | 0.0231* |

occurred at higher rates in significantly more of these experimental dyads. Experimental adult female => immature female affiliation occurred at higher rates in 68% of the comparisons ($p < .05$, Table 9). Presenting and mounting occurred at higher rates in significantly more of the experimental dyads. Experimental immature female => adult female affiliation occurred at higher levels in 66% of the comparisons ($p < .05$, Table 10). Presents of immature females to adult females occurred at higher rates in significantly more experimental dyads.

DISCUSSION

Previous Familiarity

Previous familiarity was greatest between the control dyads (Rasmussen, 1993). In heterosexual dyads this was associated with more affiliative and sexual behavior (counter to hypothesis 1) and with more heterosexual liaisons (counter to hypothesis 3). Since hypotheses 1 and 3 were confirmed and hypothesis 2 was rejected, any influences of previous familiarity not removed with statistical control would have biased the data against this pattern of results. Differences between groups in previous familiarity between subjects therefore seems an unlikely cause of our results.

Hypothesis 1

Higher rates of affiliation and sexual behavior appear to be linked causally with reproductive failure. The repeated nonpregnant estrous cycles of the experimental females, and the conception and resultant gestation of their controls, were probably the major factors responsible for differences between groups.

The majority of heterosexual interactions in the experimental group were more affiliative and sexual by 9 of the 10 variables for all group members (Table 2). For adults the majority of heterosexual interactions were more affiliative and sexual in the experimental group for all 10 variables (Table 3).

These differences between groups gave a qualitative impression as great as that between different species of macaques. The experimental group was more heterosexually and sexually oriented. Yet the control group was not asexual. Heterosexual affiliative and sexual behavior remain salient and important aspects of social organization during periods when females cannot conceive (Chapais, 1986; Hill, 1986). There was a much greater difference between groups in adult male => adult female than adult female => adult male interactions. Group differences may therefore hinge more on differences in attractiveness and receptivity of the adult females than on females' proception.

Evolutionary theory added to the ability to predict group differences. Evolutionary theory also suggests the ultimate cause of the differences: Individuals in the experimental group continue to attempt behavioral patterns that have been selected since they could lead to conception in an intact group. The answer to the functional question: "Why is there more affiliative and sexual behavior in the experimental group?" is that group members have failed to reproduce but continue in

the attempt.

Hypothesis 2

Hypothesis 2 was not confirmed: there was less affiliation between only 55% of the experimental male dyads (Table 5). Hypothesis 2 was based on a theoretical continuum of the degree to which interactions are competitive or beneficial. The theory requires the net result of interactions between the experimental males to be more competitive. In retrospect the theory does not exclude the possibility that individuals who compete more also engage in more affiliation. Hypothesis 2 is therefore revised to predict a greater ratio of competitive to beneficial behavior in the experimental group. When analyses are focused on the interactions between the 5 and 4-year-old males, there were higher levels of affiliation between adult experimental males in 92% of the comparisons between groups. The adult males may have engaged in more conciliatory and reconciliatory affiliative behavior (de Waal & RenMei, 1988) because of more intrasexual competition in the experimental group.

In dyads composed of an immature and an adult male, 81% of the comparisons between matched dyads were in the direction predicted. Lower levels of affiliation between the immature male and the adult males in the experimental group may have been due to the immature male's inability to make serious reprisals to the frequent vicious attacks by adult males.

Hypothesis 3

Hypothesis 3 was confirmed for eight of the nine variables to which it was applied in all heterosexual pairs and for all nine variables for adult heterosexual pairs. Affiliative and sexual interactions occurred between more pairs in the experimental group. The experimental females had repeated nonpregnant menstrual cycles. The greater opportunities for sexual behavior in this group may have been a proximate cause of the greater number of partners in affiliative and sexual liaisons. It would, of course, be possible for the increased sexual behavior in the experimental group to have been instead associated with more frequent sexual and affiliative behavior between the same pairs.

Affiliation Between Females

There was more affiliation between experimental females primarily because of higher levels of affiliation between the adult and immature

females (Tables 8, 9 and 10). Increased presenting and mounting could be associated with higher levels of intrasexual competition between the adult and immature females. Female intrasexual competition seems likely to be greater due to the higher levels of affiliative and sexual behavior that occurred between the adult males and immature females in the experimental group.

Replication

Comparisons have often been made between two groups of nonhuman primates (Keverne, Meller, & Martines-Aria, 1978; Rasmussen 1984). Comparisons have been made when the groups are not closely matched or are composed of different species (Gordon, Bernstein, & Rose, 1978; Rosenblum & Pauly 1984). Such comparisons have been subjected to statistical test (de Waal & RenMei 1988; Boccia 1989). The significant differences are, however, based on only two groups. The generality of the results of this, and other such studies, must therefore be regarded with caution.

This study must be replicated to determine the degree to which the hypotheses may be generalized to other groups of rhesus, and, with suitable modification, to species with different modal patterns of social organization (Rasmussen, 1981a). As R. A. Fisher (1951) noted: "In order to assert that a natural phenomenon is experimentally demonstrable we need, not an isolated record, but a reliable method of procedure". This paper describes such a method for comparison of reproductive and non-reproductive groups. Replicates, further comparative studies, and long term studies conducted on nonhuman primates certainly seem important for increased understanding of both proximate and selective consequences of the widespread use of contraception on human social behavior.

Potential Relevance to Human Behavior

In developed nations the mean number of children born per woman has steeply declined and the mean age at which a woman bears her first child has steadily increased over the past century (Short, 1974; May, 1978; Caldwell, 1982). Strong and consistent correlations have been found between changes in the number of children born by women and many changes in our premarital and marital social and sexual behavior as well as marital stability and duration (Thornton, 1977; Zelnik & Kantner, 1980; Clayton & Bokemeier, 1980; Rasmussen, 1981a; Lodewijckx, 1987; Martin & Bumpass, 1989). Decreased number of children born to women has, for example, been shown to be positively

correlated with decreased marital duration and stability (Rasmussen, 1981a). These are undoubtedly some of the most profound and far reaching changes in the natural history of the human animal within the last several centuries. These changes are similar in magnitude to other major alterations in the course of human history such as the industrial revolution, the rise of the nation state and global communication networks.

The decline in number of children born per woman, and increased age upon birth of their first child, is associated with modern fertility control methods that sever causal links between sexual and social behavior and reproduction (Montagu, 1969). It would not be ethical to conduct studies on many of the relationships between human reproduction and social behavior. When human studies are not ethical, studies conducted on nonhuman primates may sometimes contribute to comparative knowledge on biological processes similar to those in humans (Hinde, 1974). This experimental study suggests that the correlations between increased use of fertility control, decreased family size, and increased sexual interactions may be causal.

With further studies we may eventually have a strong theoretical and empirical understanding of the behavioral processes responsible for differences between groups of nonhuman primates in which sexual behavior has been uncoupled from reproduction and reproductive groups. This knowledge seems likely to increase our understanding of how differences in numbers of children born to women are linked with affiliative, sexual and marital differences between human populations. Without such an understanding, results from studies of natural reproductive groups of nonhuman primates (e.g. Rasmussen, 1979; de Waal, 1982; Goodall, 1986) are of limited use for understanding behavioral processes observed in human populations using effective means of contraception.

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STATE ORGANIZATION AND ACTIVITY IN INFANT CEBID MONKEYS (*CEBUS* AND *SAIMIRI*) IN TWO REARING CONDITIONS

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ABSTRACT: Behavioral states and their organization in 5-week old squirrel monkeys and 8-week old capuchin monkeys was evaluated. Infants at these ages are not quite at the threshold, under species-normal rearing conditions, of independent locomotion. Two age-matched infants of each species were observed continuously for a 5-day period while cared for by their mothers in their natal social groups, or while cared for by humans and housed in an incubator on a stationary support. All four infants spent similar proportions of time sleeping, drowsy, nursing, and awake. Hand-reared infants were more frequently awake and active with their hands, cocked their heads more often, and slept in shorter bouts than their mother-reared counterparts. All infants exhibited a positive correlation during the daylight hours between the duration of time in an alert quiet state and the duration of time being moved by a carrier. In addition to providing detailed information about the temporal characteristics of state organization and activity within subjects, the findings suggest the kinds of alterations in activity which can result in these species when artificial (largely stationary) rearing regimes are experienced. Many of the alterations can be interpreted as compensatory self-stimulation. The alterations are apparently different in the species studied here from those described for other species, principally macaques, experiencing similar artificial rearing regimes.

The focus of this report is the temporal organization of behavioral states and activity in infant monkeys. One aim is to provide some detailed information for species not well represented in this literature. A second aim is to consider in a preliminary fashion if rearing regime (maternal, species-normal; or by humans, called hand-rearing) affects the temporal organization of behavioral states and activity in young monkeys in the short term. We were particularly interested to see if (a) durations and rhythmicity of states and (b) frequency of activity would be influenced by rearing regimes.

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The relationship between rearing condition and the occurrence of head-cocking was of particular interest in this study in regard to the second aim. In head-cocking, an individual rotates its head distinctly about the longitudinal axis of the body while orienting in a fixed direction (Menzel, 1980; see Figure 1). Head-cocking is commonly observed in both species used in this study, as in other small-bodied nonhuman primates such as marmosets and galagos (Rogers et al., 1993; Menzel, 1980). Menzel (1980) suggested that head-cocking, a behavior particularly characteristic of young individuals still carried by another, is influenced by the infant's non-locomotor status. Menzel suggested that this might occur because head-cocking produces self-guided shifts in the visual field that aid the pick-up of visual information. Non-locomoting individuals might obtain visual information from head-cocking that they would be otherwise unable to obtain. If head-cocking is performed to increase the amount of visual information available to an infant that can not readily move the rest of its body, then it ought to be more frequent in hand-reared infants than in mother-reared infants. Hand-reared infants are even less exposed to varying visual stimulation than are passively carried, but frequently moved, mother-reared infants.

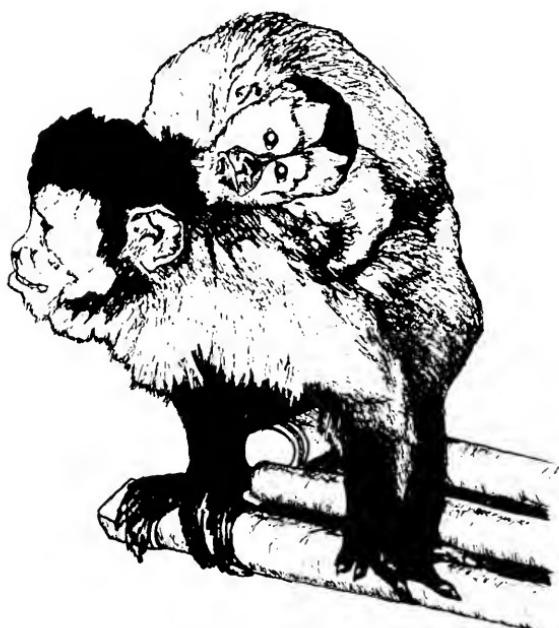


Figure 1. Sketch of a mother-reared capuchin infant displaying head-cocking. Drawn by Deborah Custance from a photograph.

Two species of monkeys (squirrel monkeys, *Saimiri sciureus*, and tufted capuchin monkeys, *Cebus apella*) were studied. These are both intermediate-sized South American monkeys exhibiting similar locomotor and developmental patterns, although motor milestones are reached more slowly in capuchin monkeys compared to squirrel monkeys (Fragaszy et al., 1991). One infant monkey of each species was studied under each rearing condition (hand or mother) in this study. Obviously, this design has limited statistical power. Nevertheless, the findings can alert us to the nature of behavioral consequences one could expect to see in subsequent studies of rearing effects with these species.

METHOD

Subjects

Four infant monkeys were studied. The two infant capuchins (both females) were observed at 50 through 54 days of age. The two infant squirrel monkeys (hand-reared: female; mother-reared: male) were observed at 36 through 40 days of age. These ages correspond to a similar period in the development of infants of the two species: they occur near the end of the pre-locomotor phase, during which infants are carried continuously. All the infants were in good health, and were phenotypically normal for their species in size, weight, and general behavioral abilities. Locomotor development of the hand-reared infants was in line with that reported by Elias (1977) for nursery-reared infants of these species; none of the infants exhibited competent quadrupedal locomotion during this period.

The mother-reared infants were cared for by their mothers in their natal social groups. The group of squirrel monkeys contained 16 other individuals, in addition to the infant subject; the group of capuchin monkeys contained 6 other individuals. Each group was housed in an enclosure with an indoor room 1.5m x 2.3m x 2.3m, connecting with an outdoor pen 3.5 x 3.5 x 2.3m. Both parts of the cage were fitted with perches at multiple heights, straw bedding, and water and food were available ad libitum. The indoor portion of the home cage was partially lit by natural light, and also had a 12 hour on/12 hour off cycle of fluorescent white lighting. Artificial lighting came on at 7 AM and went off at 7 PM. This study took place in the summer months, so that the natural light cycle was about 14 hours light:10 hours dark. The natural light arrived before, and lasted past,

the artificial lighting. During full darkness, a red light was lit in both indoor and outdoor portions of the home cage for observational purposes. Both groups were fed at about 9 AM and again at about 3 PM, and the cages were cleaned on the same schedule in each group.

The two hand-reared infants were housed in a room with natural lighting through a window, and a similar schedule of artificial lighting as the group-housed infants. The two infants had been born 6 days apart. The capuchin infant was separated from its mother two weeks after birth; the squirrel monkey, 2 days after birth. They lived together in a transparent hospital incubator which was kept at about 29 degrees C. Each infant was placed on a soft, cylindrical, stationary object (a paint roller, with long nap, mounted at a 30 degree angle from horizontal). Each infant was removed from the incubator and held for feeding at 2 to 3-hour intervals around the clock. The hand-reared infants were fed a commercial human infant formula using a pet nurser. During night-time feedings (about 10 min per infant per feeding), a shaded lamp with a 30-watt incandescent bulb was lit. For the remainder of the night, a red light was used. Infants also rode for 10 - 20 minutes at a time several times each day on the caregiver's arm while the caregiver moved about normally with the arm held in a largely horizontal position. This rearing regime had been in place for several weeks before these observations began.

Procedure

A team of trained observers, each conducting a 3-hour shift, observed each infant continuously for a period of five days (120 hours). Using a keyboard data collection device, the observer scored changes in the infant's state (sleeping; drowsy; alert inactivity, called Alert-Quiet; and alert activity, called Alert-Active; see Table 1), the onset and termination of movement by the mother, or by the human caregiver, and the occurrence of manipulative activity and head-cocking by the infant. The data were collected with a temporal accuracy of .6 seconds (1/100 minute). A three-second rule was used to determine transitions in state.

Prior to data collection, observers practiced scoring the behavior of older group-living infants of each species, and conducted simultaneous observations for purposes of determining inter-observer reliability (set at 85% agreement on total duration or frequency per variable over a 30 min session). Subsequent comparisons of data indicated no consistent variation across observers for any subject.

Table 1. Behavioral categories and defining characteristics

| Category | Defining characteristics |
|------------------------------------|--|
| 1. States | |
| Sleep | Eyes closed, body limp, twitching and change in position possible. |
| Drowsy | Eyes partly open, eyes may be glazed, some slow postural adjustments possible. |
| Alert-Quiet | Eyes wide open, head may be up or supported, body supported. May change position of arms and legs, but not of the core of the body. |
| Alert-Active | Moving the whole body, either in space as in locomotion, or in orientation, and more than a movement equivalent to changing positions on the mother. Also, when the body core is not supported (as in standing). |
| 2. Other activities with durations | |
| Movement by Mother | Mother reared: Mother locomoting or moving vigorously (as in scratching with a leg). Hand-reared: Riding on a human arm, and the arm is moving. |
| Nurse | Mother-reared: In the nursing position. Hand-reared: On the nipple |
| 3. Events | |
| Manipulate | Chew, pull, reach toward, and hold objects. Can occur in Drowsy, Quiet, or Active states. |
| Head-Cock | Abrupt movement of head about the longitudinal axis of the body. Occurs in visual inspection during Alert states. |

Analysis

Most analyses were done by individual subject. The data were first divided into 120 50-min blocks. Subsequently, the data were plotted by 24 hour units, pooling across days, for visual inspection. Spectral analyses and Box-Jenkins time series analyses (using the BMDP statistical package) were run on the duration variables expressed as % total time per block to identify periodicities in the occurrence of behavioral states. Head cock and manipulation were omitted from these analyses, as they had no meaningful duration. Spectral analyses indicate how much of the temporal variability across the 120 hours derives from multiple cycles (say, from 2 hour cycles interacting with 24 hour cycles). We first plotted the unfiltered data, and re-plotted it using filters to smooth out 24-hour cycles. The values reported below were obtained with a filter band width of .0583.

Box-Jenkins analyses indicate the strength of various temporal cycles in a particular behavior by using a correlational approach. A preliminary analysis using an autoregressive model on the original data indicated that the data were not stationary. Therefore, a 24-hour differenced series (moving average model) was derived for each variable. Last, Pearson product-moment correlations were used to examine the relationship between the proportional duration of passive movement and the infants' activity over the 120 blocks, and over the 60 daylight blocks.

Average durations per bout for the 6 duration variables (four states, plus Nurse and Movement by Mother) and the frequency of bouts for all 8 behavioral variables were graphed for visual inspection. Comparisons between hand-reared and mother-reared infants of the same species for frequency and duration variables are descriptive only; inferential comparisons are not appropriate as the frequencies in each class (subject) are drawn repeatedly from the same subjects.

RESULTS

Time budgets

Each infant's overall time budget is displayed in Figure 2. Overall, certain similarities are evident: all 4 infants spent about 40% of all their time asleep, about 7% of their time drowsy, less than 5% of their time nursing, and the remainder (nearly 50% of their time) in an alert state. Neither of the hand-reared infants engaged in stereotypical body-rocking at any time.

The capuchin mother moved during one-third of her time; the squirrel monkey much less (about 13%). The hand-reared infants were passively moved about 6% of the time, less than half the amount of time that either of the two mother-reared animals experienced movement. Even so, this amounts to one hour and 45 minutes of movement per infant per day, which is substantially more than would be experienced by a monkey infant in a standard nursery setting in which infants are not moved passively except during feeding and cleaning procedures. In this sense, our rearing regime represents a half-way point between no movement stimulation and mother-rearing.

Periodicities

The time budget data are displayed across 24 hours in Figure 3. Visual inspection of these graphs suggest that all infants exhibited

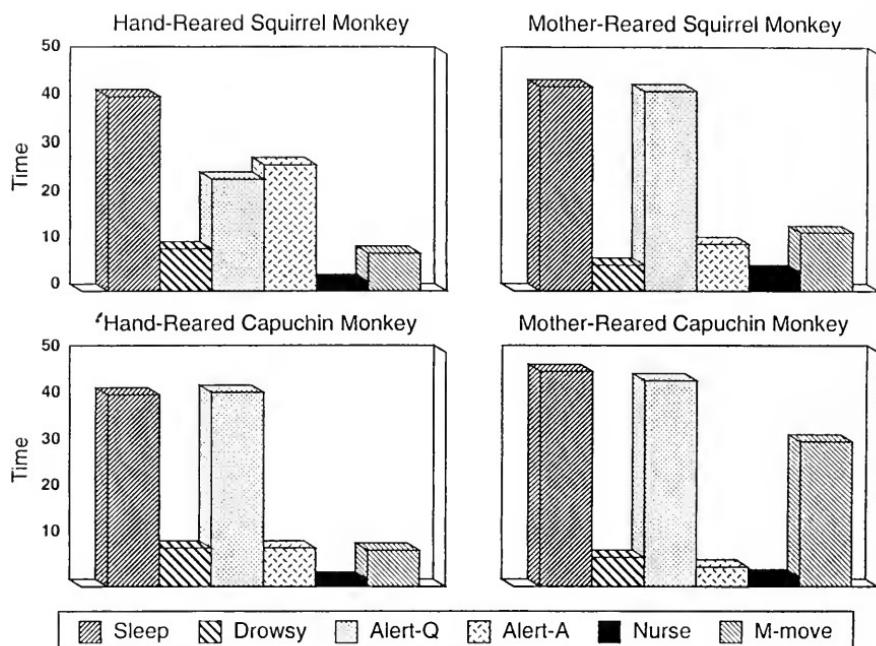


Figure 2. The distribution of time over 120 hours of observation per infant among the four states (Sleep, Drowsy, Alert-Quiet, and Alert-Active) and to two other (non-exclusive) categories (Movement by the mother or carrier, and Nurse).

strong cyclical variations in activity. Time series analyses revealed that all infants exhibited significant 24-hour periodicities in Sleep (correlation = .35 to .48). [The sign of the correlation is uninformative, and is omitted; all of these values exceed a 95% confidence interval.] As shown in Figure 3, across all five days the mother-reared infants appeared to have sleep cycles more in synchrony with day/night cycles, in that the hand-reared animals shifted the peak of sleeping from midnight to mid-day. This is most evident in the hand-reared capuchin monkey.

Other behaviors showing 24-hour periodicities were Alert-Quiet (.30 to .45), and Manipulation (.26 to .46). Three of the four monkeys exhibited a 24-hour periodicity in Alert-Active (.40 - .56). The fourth, the hand-reared capuchin monkey, did not. The two monkey mothers exhibited strong 24-hour periodicity (.55, squirrel monkey, and .59, capuchin monkey) in moving. The human carriers also showed 24-hour periodicity in carrying, although it was not as strong for movement by the monkey mothers (.33 to .38). Nursing

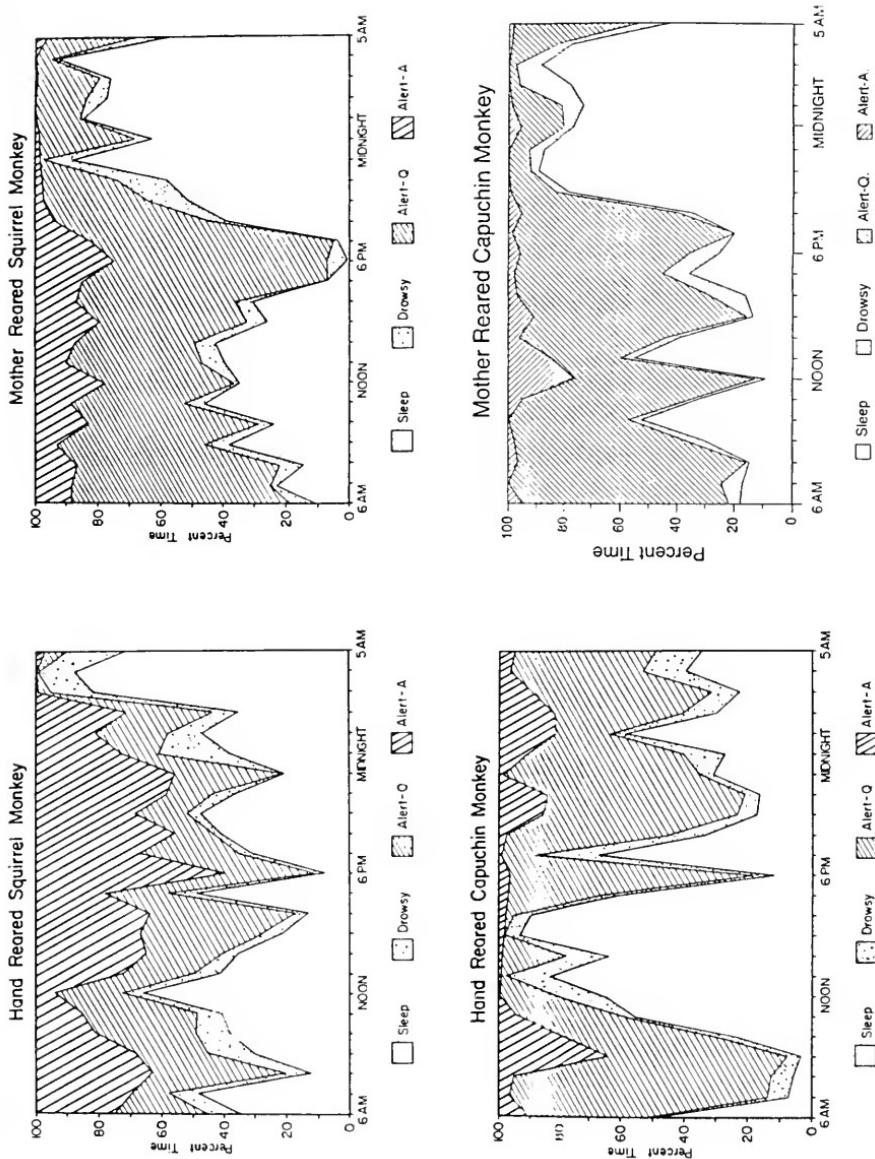


Figure 3. The distribution of time per infant among the four states across 24 hours.

showed a 24-hour periodicity for two animals, the mother-reared squirrel monkey and the hand-reared capuchin monkey. Overall, Nursing was the least periodic of all the behaviors in terms of the Box-Jenkins analyses. All four subjects exhibited 2 or 3 quite short periodicities of 2 to 5 hours in the spectral analyses of nursing.

Out of 54 periodicities exceeding the 95% confidence interval calculated by the Box-Jenkins analyses of all behaviors, 5 were for periods from 25 to 28 hours; all the rest were for 24 hours or less. For example, all four infants displayed 3 or more periodicities in Sleep of 12 hours or less with correlations of between .2 and .3. Clear differences in the extent of periodicity between hand-reared and mother-reared infants were not evident.

Correlation between infant's activity and passive movement

Strong negative correlations ($r_{xy} = -.34$ to $-.71$, $n = 120$, $p < .002$) were evident for all subjects for the duration per hour spent sleeping and being moved, and strong positive correlations between Alert-Quiet and being moved ($r_{xy} = +.32$ - $.73$, $n = 120$, $p < .001$, all cases). Nursing was strongly positively correlated with movement for the hand-reared infants, reflecting the caretaker's typical pattern of feeding the infant and then carrying it for a time afterward ($r_{xy} = +.30$ - $.40$, $n = 120$, $p < .001$, both cases). No other clear trends were evident in the correlational data for being moved with other variables. When the data for the daylight hours only (6 AM to 6 PM) were considered, the strong correlation between Alert-Quiet and movement was retained, and the values were highest for the two mother-reared individuals ($r_{xy} = +.49$ and $+.51$, mother-reared; $+.35$ and $+.39$, hand-reared; $n = 60$, all cases).

Short-term organization of behavior: Duration and frequency of bouts

The average durations per bout of the 6 state variables are given in Figure 4, and the frequency of bouts per day for all variables in Figure 5. The similarities across infants are more apparent than the differences. However, a striking difference between mother-reared and hand-reared infants is evident in the duration of sleeping bouts: Hand-reared infants sleep in shorter bouts than mother-reared infants. Also, bouts of Alert-Quiet were shorter in the hand-reared capuchin infant than her mother-reared counterpart. Surprisingly, the duration per bout of passive movement was nearly the same for all infants. The similarity of durations per bout for infants of the same species for

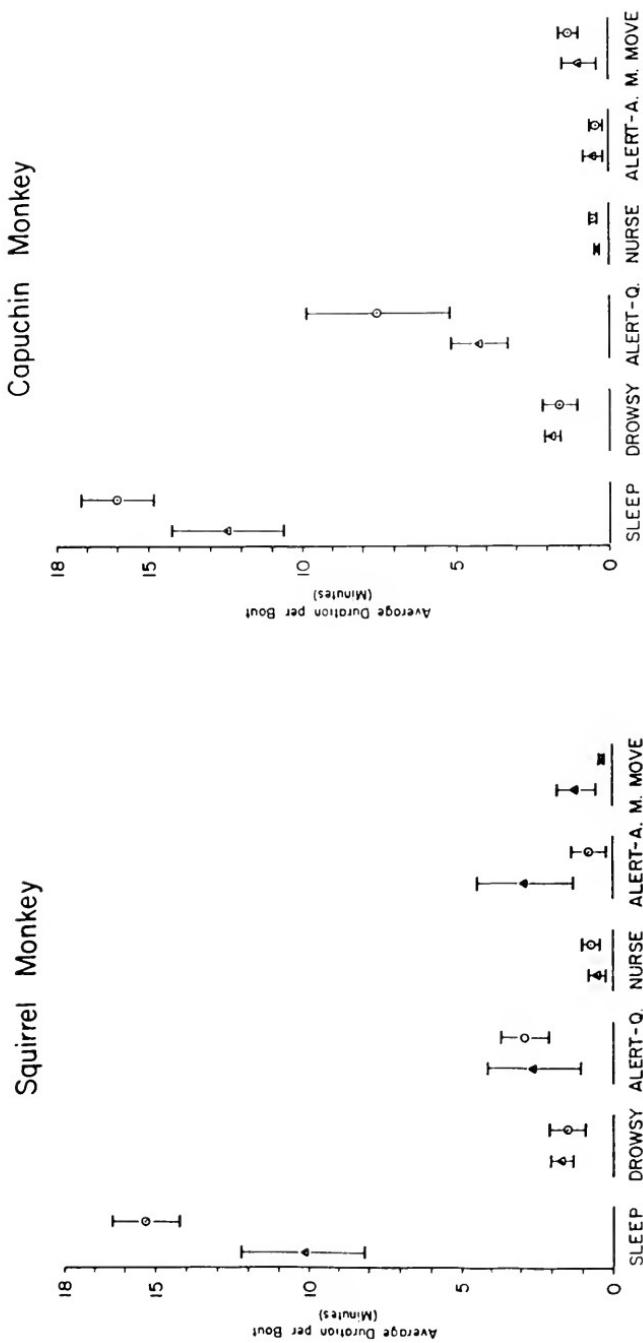


Figure 4. Average duration per bout for each activity or state per infant. Bars indicate standard deviation.

Circle = mother-reared. Triangle = hand-reared

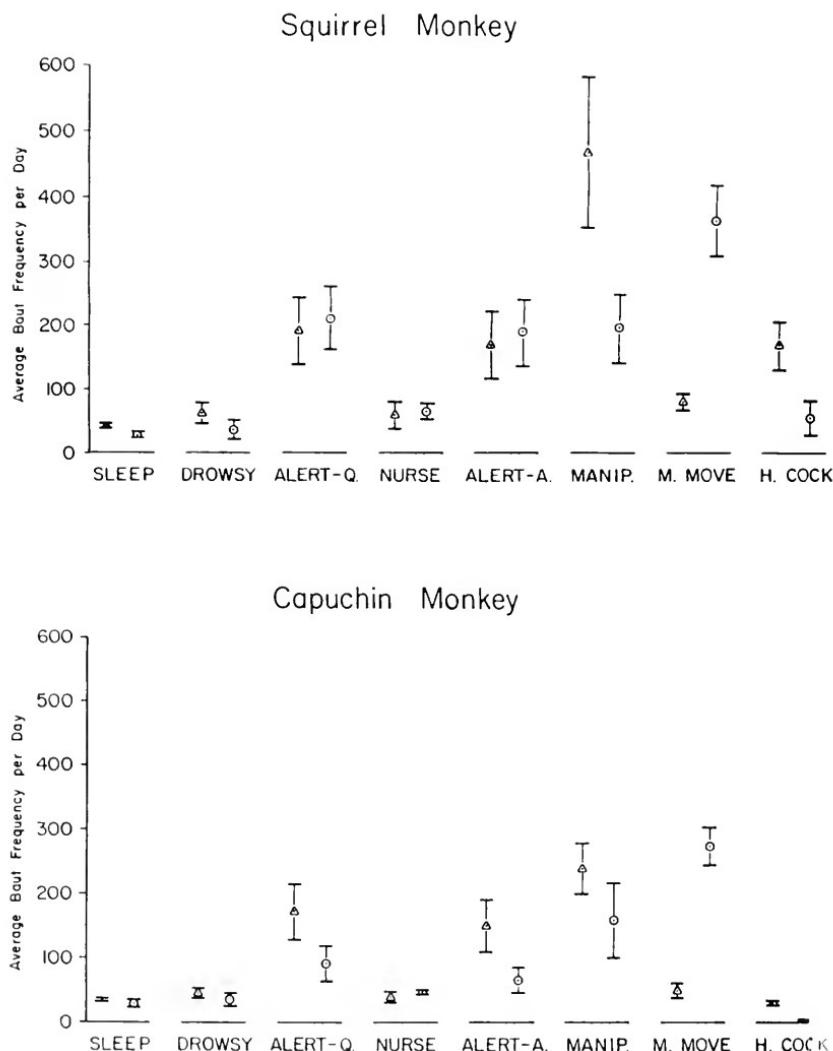


Figure 5. Average frequency per day for bouts and events per infant. Bars indicate standard deviation. Circle = mother-reared. Triangle = hand-reared.

all variables except sleep suggests that cycling through activities while awake is relatively stable in infants.

Frequencies of bouts varied in different ways than duration of bouts. The greatest differences between the capuchin infants occurred in Alert-Quiet, with the hand-reared infant entering this state more

frequently (but as we saw above, for shorter durations) than the mother-reared infant (167 vs. 85 times per day). The hand-reared infant also entered an Alert-Active state more frequently than the mother-reared infant (150 vs. 65 times/day). The mother-reared infant was moved passively much more frequently than the hand-reared infant (272 vs. 50 times/day).

The two squirrel monkeys displayed similar bout frequencies for most variables, except for frequency of bouts of passive movement. The differences in the frequency of bouts of passive movement were roughly the same as for the capuchins: Much greater frequencies were observed in the mother-reared infant than in the hand-reared infant (360 vs. 75 times/day).

Frequency of head-cocking and manipulation

The mother-reared capuchin infant was rarely seen to cock its head (.1 times per hour while the infant was awake). This behavior occurred regularly (2.6 times per hour while the infant was awake) in the hand-reared capuchin infant. The hand-reared infant also engaged in manipulation somewhat more frequently than her mother-reared counterpart (12 times per hour for the mother reared infant; 17 for the hand-reared infant, for the time spent awake or drowsy).

A large difference was evident between the two squirrel monkeys in the frequency of manipulation and head-cocking (each more than twice as frequent in the hand-reared infant as in the mother-reared infant). Head cocking was much more frequent in both of the squirrel monkeys than in either capuchin (4 times per hour, hand-reared squirrel monkey, and 14 times per hour, for mother-reared squirrel monkey, for hours awake or drowsy). Manipulation occurred 33 times per hour while awake in the hand-reared squirrel monkey, and 14 times in the mother-reared squirrel monkey.

DISCUSSION

Although the single-subject design of this study limits the strength of the conclusions to be drawn, a few findings stand out. The four young monkeys in this study exhibited similarly strong rhythmicity in states and in overall time budgets, despite variations among them in species and rearing conditions. These aspects of behavior may reflect intrinsic regulatory processes which are impervious to all but the most extreme environmental variations. Undoubtedly, however, they

undergo dramatic developmental change; this aspect of variation warrants its own investigation (Fragaszy 1989, 1990b; Wolff 1987).

Second, the infants varied more substantially in the frequency of particular activities and in the duration and frequency of bouts of active states than in rhythmicity or overall time budgets. Considering rearing differences first, the species-atypical rearing regime experienced by the two hand-reared infants in this study, while relatively "enriched" with regard to the extent of contact with an animate caregiver and the provision of passive movement, was still associated with significant alterations of the infants' behavior and experience of movement. Infants reared with their mothers engaged in fewer bouts of manipulation and head cocking, and longer bouts of sleeping than their hand-reared counterparts, and they experienced more passive movement and more frequent bouts of passive movement.

Although the absolute frequency of head-cocking observed in this study in mother-reared infants was much lower than in Menzel's (1980) study, the difference between the species were the same as he observed: Capuchins head-cocked less frequently than squirrel monkeys. Two infant squirrel monkeys observed longitudinally by Menzel exhibited their greatest frequency of head cocking at 6 and 8 weeks of age. Thus it seems likely that we sampled the squirrel monkeys' behavior at an optimal age to observe this behavior. We are able to rule out the possibility that the difference between infants of the two species in this study is a function of when observations occurred in relation to a developmental pattern of waxing and waning of this particular behavior. Head cocking has been observed in a capuchin infant as early as 4 weeks of age, and two capuchin infants followed longitudinally from 6 weeks through 24 weeks head-cocked in all weeks at rates similar to those observed in the mother-reared infant in this study (England et al. unpublished data). Differences between the frequencies observed in this study in the squirrel monkeys and those observed by Menzel (1980) may be a function of the rate at which novel objects or other interesting visual stimuli came into view in the two studies. Rogers et al. (1993) show that the novelty of the object to be viewed strongly affects the occurrence of head-cocking in galagos (*Galago*).

The more important result, however, for the present purpose is that head-cocking occurred significantly more frequently in the hand-reared infant of each species than in its mother-reared counterpart. Hand-rearing apparently elicits atypically high frequencies of this species-normal behavior in both species. This

finding is consistent with Menzel's (1980) hypothesis that head-cocking is a behavioral mechanism to increase visual acuity while in a static posture through self-guided shifts in the visual field. Head-cocking also provides vestibular stimulation, which could be pleasureable in its own right, particularly if such stimulation from other sources is limited.

Manipulation was also more frequent in the hand-reared infants than in the mother-reared infants. Manipulation is more likely to be liberated by hand-rearing than elicited, as head-cocking seems to have been. Postural constraints faced by young infants riding on an unpredictably moving carrier limit the individual's ability to let go of the supporting surface and to reach away from the carrier towards objects in the near environment. However, when supported on a stationary surface, infants of both species exhibited precocially high frequencies of manipulative activity. These findings are reminiscent of those by Thelen and colleagues (Thelen and Ulrich, 1991) and Rochat and Bullinger (in press), among others, with human infants. Given appropriate postural support, human infants in the first 6 - 12 months of life have displayed motor coordination in walking movements and reaching for objects that, in older infants, are enabled by maturing postural control.

After the frequencies of head-cocking and manipulation, perhaps the largest difference between hand-reared and mother-reared animals occurred in the timing of sleeping. Mother-reared animals slept mostly at night; hand-reared animals slept more during the daylight hours. Some increase of sleeping in the daylight hours is to be expected given that the hand-reared animals were on a two-hour feeding schedule around the clock, and our feeding procedure required that we waken the infant sufficiently to bottle-feed it. We did not know when we began the study whether mother-reared infants of these ages normally go through the night without nursing. Our findings on the periodicity of nursing suggest that in natural situations they do nurse at night about as often as we fed the hand-reared infants, but our sleeping data suggest that they wake only briefly to do so.

These findings suggest that some elements of behavioral organization are more labile than others in response to the complex of features varying between mother-rearing and hand-rearing as we practiced it. Except for differences in the duration of sleeping bouts and when sleeping occurred, the labile elements (frequency of manipulation, head cocking, and bouts of Alert-active and Alert quiet; duration of bouts of Alert-active and Alert-quiet) share the common

theme of more frequent self-produced stimulation on the part of the hand-reared infants. Differences in movement stimulation are likely to be one important source of the differences between mother-reared and hand-reared infants in the frequency of self-stimulatory activities. This hypothesis awaits direct experimental verification. The differential availability of objects and surfaces to contact close at hand (probably greater for hand-reared animals) or in the appearance of novel visual stimuli (probably greater for mother-reared animals) may be other sources of the differences in the distribution of manipulation and head-cocking. These alternate hypotheses could be tested.

Perhaps one reason why the short-term consequences of altered rearing environments on the organization of activity in infant monkeys have not been given more attention is the virtual restriction of data on this topic to one genus (*Macaca*). Activity differences between hand-reared and mother-reared macaques are not striking. In both rearing settings, young macaques begin to move independently in the first to second week of life, and in both settings they habitually pick up objects in the mouth until postural control enables a hand to be used for this purpose. Buccal prehension appears at about 7 days of age in Japanese and crabeating macaques (*M. fuscata* and *M. fascicularis*, respectively; Poti, 1989). Rhesus infants without external postural support are able to reach through an aperture and prehend small objects such as string within the first three weeks of life (Mason, Harlow, and Reuping, 1959). Schneider and Suomi (1992 b) report that the composite scores for activity (obtained at several points during the first month of life) did not vary across groups of rhesus infants undergoing varying hand-rearing regimes. Similarly, Schneider et al. (1991 a) report that different hand rearing conditions did not influence activity in the home cage in rhesus infants across the first year of life, although they did affect reflexes, muscle tone, and irritability. Comparisons of hand-reared and mother-reared macaques do not suggest obvious differences in age at reaching various motor milestones (compare Hinde et al., 1964 with Castell & Sackett, 1973 or Mowbray & Cadell, 1962). In short, the similarities of behavioral organization and form in macaque infants reared in varying circumstances do not invite further study of the short-term alterations of behavioral organization produced by nursery rearing, as few alterations are noticeable.

The findings of this study suggest that hand-rearing impacts behavioral organization in the short run in infant squirrel and capuchin monkeys in ways that have not been mentioned for infant macaques (see also Fragaszy 1990a, 1990b). It is not clear that these impacts

are not evident in macaques, because they have not been sought specifically, but the general picture of infant activity during hand-rearing provided by earlier studies does not suggest their presence. If they are not present, it is probably in part because of the different affordances of artificial rearing environments for macaques than for New World monkeys. Infant macaques can locomote much sooner after birth, and for the first few months of life are less reliant than New World monkeys on external postural stability to enable prehensile activity. They also exhibit an alternative method (buccal prehension) of grasping objects while postural control is limited. Thus frequency of tactile or prehensile exploratory activity is less likely to be affected in macaques than in New World monkeys by movement or postural support conditions. For all these reasons, and perhaps others not considered here, macaques can be expected to exhibit fewer or less obvious immediate behavioral adjustments to largely stationary rearing regimes than are New World monkeys.

The most general conclusion to be drawn from these findings is that when species-normal behavior in infancy is desired, careful consideration should be given to the implementation of rearing regimes for infant monkeys during the period in which they are unable to locomote, and for New World monkeys, this can be several months. For non-locomoting infants, movement stimulation is an obvious feature of the rearing environment to consider.

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